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The effect of area and isolation on insular dwarf proboscideans

Alexandra A. E van der Geer
Netherlands Biodiversity Center Naturalis

Gerrit D. van den Bergh
University of Wollongong, gert@uow.edu.au

George A. Lyras
National and Kapodistrian University of Athens

Unggul W. Prasetyo
University of Wollongong

Rokus Awe Due
National Research Center for Archaeology, Indonesia

See next page for additional authors

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Abstract

Aim We investigated the hypothesis that insular body size of fossil elephants is directly related to isolation and surface area of the focal islands. **Location** Palaeo-islands worldwide. **Methods** We assembled data on the geographical characteristics (area and isolation) of islands and body size evolution of palaeo-insular species for 22 insular species of fossil elephants across 17 islands. **Results** Our results support the generality of the island rule in the sense that all but one of the elephants experienced dwarfism on islands. The smallest islands generally harbour the smallest elephants. We found no support for the hypothesis that body size of elephants declines with island isolation. Body size is weakly and positively correlated with island area for proboscideans as a whole, but more strongly correlated for Stegodontidae when considered separately. Average body size decrease is much higher when competitors are present. **Main conclusions** Body size in insular elephants is not significantly correlated with the isolation of an island. Surface area, however, is a significant predictor of body size. The correlation is positive but relatively weak; c. 23% of the variation is explained by surface area. Body size variation seems most strongly influenced by ecological interactions with competitors, possibly followed by time in isolation. Elephants exhibited far more extreme cases of dwarfism than extant insular mammals, which is consistent with the substantially more extended period of deep geological time that the selective pressures could act on these insular populations.

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

Authors

Alexandra A. E van der Geer, Gerrit D. van den Bergh, George A. Lyras, Unggul W. Prasetyo, Rokus Awe Due, Erick Setiyabudi, and Hara Drinia

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2 **PROBOSCIDEANS**

3

4 **Authors:**

5 Alexandra A.E. van der Geer[1,2], Gerrit D. van den Bergh[3,1], George A. Lyras[2],

6 Unggul W. Prasetyo[3,4], †Rokus Awe Due[5], Erick Setiyabudi[4], Hara Drinia[2]

7

8 **Addresses:**

9 [1] Netherlands Biodiversity Center Naturalis, Leiden, The Netherlands

10 [2] National and Kapodistrian University of Athens, Zografou, Greece

11 [3] Centre for Archaeological Science, University of Wollongong, Wollongong, Australia

12 [4] Geology Museum, Bandung, Indonesia

13 [5] National Research Center for Archaeology, Jakarta, Indonesia
14 †The fifth author passed away while the article was in an advanced stage

15

16 **Corresponding author:**

17 Alexandra A.E. van der Geer, Netherlands Biodiversity Center Naturalis, Leiden, the

18 Netherlands; alexandra.vandergeer@naturalis.nl

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ABSTRACT

22

23 **Aim** We investigated the hypothesis that insular body size of fossil elephants is

24 directly related to isolation and surface area of the focal islands.

25 **Location** Palaeo-islands worldwide.

26 **Methods** We assembled data on geographic characteristics (area and isolation) of

27 islands and body size evolution of palaeo-insular species for 22 insular species of

28 fossil elephants across 17 islands.

29 **Results** Our results support the generality of the island rule in the sense that all but

30 one of the elephants experienced dwarfism on islands. The smallest islands generally

31 harbour the smallest elephants. We found no support for the hypothesis that body

32 size of elephants declines with island isolation. Body size is weakly and positively

33 correlated with island area for proboscideans as a whole, but more strongly

34 correlated for Stegodontidae when considered separately. Average body size

35 decrease is much higher when competitors are present.

36 **Main conclusions** Body size in insular elephants is not significantly correlated with

37 the isolation of an island. Surface area, however, is a significant predictor of body

38 size. The correlation is positive but relatively weak; about 23% of the variation is

39 explained by surface area. Body size variation seems most strongly influenced by

40 ecological interactions with competitors, possibly followed by by time in isolation.

41 Elephants exhibited far more extreme cases of dwarfism than extant insular

42 mammals, which is consistent with the substantially more extended period of deep

43 geological time that the selective pressures could act on these insular populations.

44

45 **KEYWORDS**

46 *Elephas*, fossil record, insularity, island biogeography, island rule, *Palaeoloxodon*,

47 Pleistocene, *Stegodon*

INTRODUCTION

Vertebrates on islands generally follow a body size trend from gigantism in small species to dwarfism in large species, a trend coined "the Island Rule" by Van Valen (1973) and subsequent authors. The many deviations from this pattern have given rise to considerable criticism regarding generality and causality of the rule: see, for example, Meiri *et al.* (2004, 2006, 2008a) for mammalian carnivores (but see Lyras *et al.* 2010), Meiri (2007) for lizards, Meiri *et al.* (2011) for birds and lizards (though they found weak support for mammals), and Itescu *et al.* (2014) for insular tortoises worldwide. A large study has investigated the generality of the island rule (Lomolino *et al.*, 2013), which, by analysing both extant and extinct mammals (including very large mammals such as elephants in the dataset), includes the important factor deep geological time under which species evolved in isolation. Context (ecological interactions, isolation, area, climate etc.) appears to be of crucial importance and differences herein can explain differences in observed body size evolution between populations of the same species (Lomolino *et al.*, 2012). The various contextual factors do not contribute equally to the eventual body mass outcome, for example, the presence of ecologically relevant competitors appears to have a higher impact than ancestral body mass and climatic variability (Sondaar, 1977; Lomolino, 1985; Raia & Meiri, 2006; Palombo, 2007, 2009; Lomolino *et al.*, 2012; van der Geer *et al.*, 2013; *inter alia* Itescu *et al.*, 2014). For example, insular elephants have been shown to have maintained a larger body mass in the presence of deer and hippo, likely because the presence of smaller-bodied intra-guild competitors prevented elephants from reaching a similar size class (Palombo, 2007).

Taxa such as murids and deer are well represented in both the fossil as well as the extant insular record. Whereas very large-bodied taxa such as elephants and

73   hippos are extremely limited in the extant record despite being common, not to say

74   typical, elements of island faunas worldwide during the Pleistocene. Elephants

75   provide some of the most spectacular cases of body size evolution in palaeo-insular

76   mammals (Fig. 1). For example, the elephant (*Palaeoloxodon falconeri*) from

77   Spinagallo Cave (Siracuse, Sicily; Middle Pleistocene) dwarfed to just 2% of the size

78   (body mass) of its mainland ancestor (*Palaeoloxodon antiquus*) (Ambrosetti, 1968;

79   Palombo & Ferretti, 2005; Lomolino *et al*., 2013).

80   Here, we expand the dataset for insular proboscideans as given in Lomolino *et*

81   *al*. (2013) and further evaluate insular size trends of these very large insular mammals

82   which are lacking in basically extant insular faunas. The dataset is limited to North

83   America and Eurasia as no fossil proboscideans have been discovered from islands of

84   Africa, South America or Antarctica.

85   In the conceptual model as proposed by Lomolino *et al*. (2012), the principal

86   selection force for (very) large mammals is ecological release. Ecological release,

87   however, is more important on smaller islands (where there are fewer

88   competitors/predators), which would indirectly introduce an effect of area on elephant

89   body size. The number of ecologically relevant competitors / predators is also related

90   to isolation, as the chance of successful dispersal is inversely related to isolation. This

91   means that both area and isolation are expected to have an indirect effect on the

92   degree of dwarfism of elephants through ecological release.

93   The effect of factors associated with thermoregulation (e.g. island latitude,

94   temperature and seasonality) is potentially relevant, but will not be tested here as the

95   variation in climatic variables, especially lowest winter temperature and rainfall,

96   across the focal palaeo-islands and the different geological periods (including glacials,

97   interglacials, and spanning the entire Pleistocene) cannot be estimated reliably.

98   The testable predictions of the ecological model of body size evolution

99 (Lomolino *et al.*, 2012) for palaeo-insular proboscideans are as follows.

100 1) Proboscideans should exhibit dwarfism on islands, following the general "Island

101   Rule" prediction that large mammals become smaller;

102 2) Body size in proboscideans should be positively correlated with island area but

103   negatively correlated with isolation. The rationale here is that both area and

104   isolation are correlated with the presence and number of ecologically relevant

105   competitors and predators: the first as a function of carrying capacity, the second

106   as a function of dispersal chances.

107 3) The degree of dwarfism should be highest in the absence of ecologically interacting

108   taxa. The presence of large to medium-sized competing herbivores and/or of

109   predators is expected to prevent dwarfism to avoid competition and/or escape

110   predation, respectively.

111

112 **MATERIALS AND METHODS**

113 **Estimation of body size and relative size index (S_i)**

114   As is detailed within Table 1, the dataset comprises 22 insular proboscidean

115 species. Because this study includes fossilised individuals, preservation is

116 inconsistent. Therefore, and of necessity, different methods for estimating body size

117 and relative size index were applied. The calculated relative size index (S_i or size

118 ratio) for each pair of insular proboscidean and its mainland ancestral species was

119 obtained by dividing the estimated body mass of the focal species by that of the

120 ancestral species (=SR in Meiri *et al*., 2008a). Body size (or mass) of insular fossil

121 species and their mainland ancestors was either estimated using taxon-specific

122 equations for estimating body masses developed by Christiansen (2004) for living

123   elephants, or taken from published sources (see Appendix S1 for details and

124   references). The alternative method of calculating ratios based on linear

125   measurements and applying the cubic law instead of indirectly via body mass has

126   been demonstrated to work equally well (Meiri *et al*., 2006, 2008a), but we preferred

127   the indirect method enabling inclusion of data from the literature and thereby

128   increasing our sample size. Parameters that were used in this study to estimate body

129   mass were the lengths of appendicular bones (humerus, femur, tibia) that provided the

130   most reliable regression results in the study by Christiansen (2004). For each species,

131   we calculated body masses based on the average lengths for each element (or one or

132   two of these elements, if not all three were available, again in order to increase our S_i

133   sample size). We then took the average of the mass estimates based on different

134   appendicular bones, assuming dependency between the different elements by absence

135   of evidence that the 'bauplan' of insular elephants had changed drastically. We found

136   that estimations of S_i based on a single element versus based on all three elements

137   produced similar results (see Appendix S1 following Table S3). We also based our

138   body-weight estimates on length measurements only (as opposed to minimum

139   circumferences of long bone diaphyses) because it has been observed that stegodonts

140   had comparatively sturdy long bones as compared to modern elephants (Hooijer,

141   1955).

142   For species for which no suitable postcranial elements were available, S_i was

143   calculated as the ratio of the cubed linear dimensions of the lower third molar

144   following Lomolino (2005). The problem with only using dental elements, however,

145   is that on geological time scales, molar dimensions have been found to lag behind in

146   the initial stages of dwarfism (Lister, 1989, 1996). This also applies to

147   palaeoloxodontine dwarf elephants, where decrease in humerus length (as a proxy for

148 body size) and molar width (as a proxy for dental size) have initially different scaling

149 rates (see Appendix S1).

150   For *Stegodon* species of which no suitable postcranial was available, but adult

151 mandibles instead, a new regression was established (see Appendix S1 Table S3).

152 This regression is derived from femur/tibia/humerus lengths against mandibular width

153 of other *Stegodon* species, for which both long bones and (fragments of) mandibles of

154 full-grown individuals could be measured (see Appendix S1).

155   The resulting dataset comprises 22 island-mainland pairs of fossil

156 proboscideans and their calculated size indices (S_i values) on 17 islands worldwide

157 (Fig. 2).

158 **Estimation of island area and isolation**

159 Island area and isolation were estimated with Global Mapper v.15 software based on

160 published data on palaeogeography, geodynamics, sea level changes, extension of

161 tectonically undisturbed marine deposits, and offshore bathymetry. For most of the

162 islands in the Wallacea region we used the map of Hanebuth *et al.* (2011) representing

163 the palaeogeography at 12.7 kyr BP, when the sea level was 60 m below present. This

164 can be considered as the 'mean' sea-level that prevailed for the longest periods of

165 time during the Quaternary (calculated from Pleistocene sea-levels as given in

166 Bintanja *et al*., 2005). A sea level of -60 m also applies to the Mediterranean,

167 following Lambeck & Chappell (2001) for the late Pleistocene. We assume here that

168 body mass evolution in proboscideans takes a considerable time, and thus likely

169 depends more on mean surface area rather than on the relatively short-lived extreme

170 values. We infer this from the observation that Holocene endemics did not reach the

171 same drastic body size decrease as Pleistocene endemics did (Lomolino *et al*., 2013).

172   Initially, dwarfism may evolve rapidly (in a few thousand years), but is then followed

173   by a second stage of slower, but ultimately much more pronounced size change

174   (Lister, 1989, 1996; van der Geer *et al*., 2013). We are aware that -60 m may be

175   somewhat arbitrary, but since we apply this level to all islands, the results are biased

176   in the same direction, and remain the same when comparing islands mutually.

177   Sumba and Timor are exceptional cases, because their late Pleistocene uplift far

178   exceeded the eustatic sea level fluctuations. The strong recent tectonic uplift of

179   Sumba has a rate of 0.2–0.5 m/kyr, as evidenced by dated raised coral terraces (Bard

180   *et al.*, 1996). We have taken the 500 m contour level (the highest coral terrace is 475

181   m above present-day sea level) to calculate the palaeo-surface area. Timor has also

182   been strongly uplifted, at least 700 m during the last 200,000 kyr (de Smet *et al.*,

183   1990), and therefore we have taken the 500 m contour as a rough estimate of the

184   middle Pleistocene coastline of Timor. Flores in contrast, appears not to have been

185   uplifted in such a dramatic way as Timor and Sumba were. The recent uplift of Flores

186   is much less substantial, as indicated by the flat lying terrestrial sediments of early

187   and middle Pleistocene age now occurring at an elevation of around 350 m above

188   present sea level (Brumm *et al*., 2010), unlike the highly uplifted Pleistocene marine

189   coralline sediments of similar ages on Timor-Sumba. We therefore have estimated the

190   area and isolation for Flores in a similar way as for most other islands, at -60 m sea

191   level.

192   The following islands have alternative values for either area or isolation (for

193   details, see Appendix S1). Crete in the early Pleistocene may have still consisted of

194   two islands as it did at the end of the Pliocene (van Hinsbergen & Meulenkamp,

195   2006), or alternatively, was already merged due to the uplift into a single island as

196   suggested by the presence of *Kritimys* in both parts. The uncertainty is caused by the

197 uncertain age of the Cretan dwarf mammoth (Herridge & Lister, 2012). Flores

198 (Pleistocene) was isolated from the mainland via Komodo, Sumbawa and Lombok or

199 alternatively, via Sulawesi and the Philippines, based on ocean currents and the fossil

200 record (Morwood & Jungers, 2009; Dennell *et al*., 2014). Luzon (late Pleistocene)

201 was part of the palaeo-island Greater Luzon (Heaney *et al*., 2005) or alternatively, its

202 northern part (where the fossils come from) constituted a separate island during much

203 of the Pleistocene, separated from the southern part by a NW-SE trending fault zone

204 (Defant & Ragland, 1988) at present bordered to the south by the low lying Central

205 Valley. Luzon (late Pleistocene) was isolated from the mainland via Mindoro and

206 Palawan or alternatively, via Mindoro, Palawan and Borneo, assuming that Palawan

207 was not connected to Borneo. Sicily (early Middle Pleistocene) still consisted of two

208 palaeo-islands, or alternatively of one larger, merged island (see palaeo-maps in

209 Bonfiglio *et al*., 2002; partially based on endemism of the fauna, implying a potential

210 circularity), which influences the estimated values for both area and isolation.

211 Furthermore, a connection between Sicily and Malta is unproven (Herridge, 2010),

212 and if a connecting ridge was ever exposed, it likely was merely a series of stepping

213 stones (van der Geer *et al*., 2010) as exposure of a continuous land bridge would

214 require a drop in sea level of at least 120 to 150 m. Because of these uncertainties we

215 have not included the Maltese material attributed to *P. falconeri* into our analysis.

216 South-western Sulawesi during the early Pleistocene still constituted a separate

217 palaeo-island or alternatively, may have been already merged with the other parts of

218 Sulawesi rather than at some stage during the middle or late Pleistocene (van den

219 Bergh, 1999).

220

221 **Taxonomic and phylogenetic framework**

222   Here, we use the generic name *Palaeoloxodon* instead of *Elephas* for the

223   Mediterranean insular and mainland straight-tusked elephants (following Shoshani *et*

224   *al.*, 2007; Todd, 2010). *Palaeoloxodon* "*mnaidriensis*", referred to as *Palaeoloxodon*

225   nov. sp. in Herridge (2010), still awaits revision. The "large-sized *Elephas*" from

226   Sulawesi (*Palaeoloxodon* sp., Tanrung Formation) is here considered conspecific

227   with, or at least identical in size to *P. namadicus* (following van den Bergh, 1999).

228   Ancestral taxa for each insular species are based on the literature (van den

229   Bergh, 1999; Palombo, 2001; Herridge, 2010; Herridge & Lister, 2012; Roth, 1982;

230   van der Geer *et al*., 2010). For mainland *Palaeoloxodon*, we use specimens from Italy

231   and Greece, that are considered ancestral to the insular populations. In case an insular

232   species was derived from a mainland taxon that must have migrated via an

233   intermediate island (Flores, Timor, Sumba), we calculated body size index relative to

234   the mainland ancestor, and not relative to the dwarfed taxon from the intermediate

235   island. Most likely, the ancestral species from the intermediate island did not disperse

236   to the island farther away following drastic reduction in body size on the intermediate

237   island, but more likely this happened relatively soon after colonization when it was

238   still large-bodied. This inference is considered the most likely scenario, because

239   smaller body size for swimming elephants would signify reduce dispersal probability

240   due to more restricted fasting endurance and reduced buoyancy (pneumatic bone

241   tissue is lost in dwarf elephants) (Sondaar, 1977).

242   The *S. trigonocephalus* sample (Java) includes various subspecies of different

243   sizes. We here only use the Trinil H.K. material, which forms a homogenous sample

244   from a single layer estimated to 0.9 Ma (van den Bergh, 1999; but 0.54–0.43 Ma in

245   Joordens *et al*., 2014), when Java constituted an island, based on the endemic

246   character of the fauna from this site (van den Bergh, 1999). The alternative scenario is

247   that Java was connected through a filtered corridor with the mainland (Larick *et al*.,

248   2000; see for an extensive discussion of pros and contras, Meijaard [2004]). Evidence

249   for at least a partial isolation is provided by the presence of the following endemic

250   taxa at Trinil H.K.: *Axis lydekkeri*, *Bibos palaesondaicus*, *Bubalus palaeokerabau*,

251   *Duboisia santeng*, *Mececyon trinilensis* (=*Cuon* in Louys, 2014; here, we follow

252   Lyras *et al*. 2010, awaiting a revision of the Javanese canids), and *Sus brachygnathus*.

253   *Palaeoloxodon leonardi* (Sicily) and *P*. sp. (Delos) are excluded because their

254   stratigraphic positions remain unresolved. This also applies to the significantly larger

255   elephant species (*P. xylophagou*) of Cyprus (Athanassiou *et al*., 2014; Athanassiou *et*

256   *al*., 2015). The indeterminate Proboscidea and *E*. or *P. beyeri* from Luzon (de Vos &

257   Bautista, 2003) are omitted because their ancestry, chronology and context are

258   insufficiently known.

259

260   **Ecological assemblages**

261   The number of competitors and predators most likely to have directly interacted with

262   the focal insular species are based on published fauna lists (van den Bergh, 1999; van

263   der Geer *et al*., 2010) for local faunal assemblages containing the focal species.

264   Judgement on the likelihood of competition or predation were based on consultation

265   of references on the diet and habitats of those species in order to determine which

266   ones were likely to be significant competitors or predators of the focal insular species.

267   Reptiles were not considered as potential interacting taxa because of their low

268   energetic demands.

269   Late middle to late Pleistocene Sicily, however, poses a problem. The dwarf

270   elephant belongs to two successive faunal units or complexes (*P. mnaidriensis* FC and

271   San Teodoro FC) (Bonfiglio *et al*., 2000). The elephant sample we use here is from

272   Puntali Cave, dated either late middle Pleistocene (c. 180 ka) or late Pleistocene,

273   comparable to that of San Teodoro (c. 32 ka) (Ferretti, 2008). We here tentatively

274   include faunal elements from both FC's, with the exception of the lion, which we omit

275   as it is restricted to San Ciro cave and Canita. Elements not retrieved from Puntali

276   Cave itself are indicated with a question mark.

277

278   **Statistical analyses**

279   We first tested for the normality of our data (body mass index, area, isolation) by

280   using the Shapiro-Wilk test (Shapiro & Wilk, 1965). Then we used 2-tailed Pearson's

281   test to check for correlations between the variables (significance level alpha=0.05).

282   For significantly correlated variables, a simple linear regression analysis (parametric)

283   was used to test for the goodness of fit (r^2; proportion of variability in the response) of

284   the correlation. We used an independent-samples' t-test to compare the insular body

285   size evolution of the various genera. Statistical analyses were performed using IBM

286   SPSS Statistics for Windows, Version 21. A 1-step ANOVA was used to test the

287   effect of the presence of competitors on body size evolution.

288   For the development of a regression to estimate body size with mandibular width

289   measurements, a reduced major axis regression on log-transformed (base 10) data was

290   used.

291

292   **RESULTS**

293   As illustrated in Table 1 and consistent with Prediction 1, body size variation among

294   insular proboscideans matches previously reported patterns for extant mammals and

295   other vertebrates and was entirely consistent with the island rule. That is, all

296   proboscidean species except one had a smaller body size than the respective mainland

297   ancestral species (n=23; mean S_i=0.28, SD=0.24). The most pronounced case of size

298   reduction is exhibited by *P. falconeri* (Sicily; S_i=0.02) and *P. cypriotes* (Cyprus;

299   S_i=0.02) for *Palaeoloxodon*, *M. creticus* (Crete; S_i=0.04) for *Mammuthus* and *S.*

300   *sumbaensis* (Sumba; S_i=0.08) for *Stegodon*. No size reduction is observed in the large

301   *Elephas* species from Sulawesi. Limited size reduction is seen in *S. trigonocephalus*

302   (Java, Trinil) (S_i=0.65). On a whole, *Stegodon* species (n=10) show a lesser body size

303   reduction (or higher S_i) than *Palaeoloxodon* (n=8), with a respective mean $S_i = 0.33$

304   (SD=0.19) and S_i=0.16 (SD=0.13). This difference is significant (t (16) =-2.20,

305   p=0.04). The number of *Mammuthus* species (n=4) is too low to be included in the t-

306   test.

307   The log-transformed (base 10) variables of surface area, alternative surface

308   area and untransformed minimal isolation were normally distributed, but maximal

309   isolation is not (for SPSS output, see Appendix S1, after Table S4). However, the

310   normality of maximal isolation is only minimally violated, and we proceed with it as

311   if normally distributed.

312   Neither minimal nor maximal isolation is statistically correlated with insular

313   body size index (Pearson R=-0.09 and -0.05, respectively, with p=0.69 and p=0.84).

314   Surprisingly, some islands within visual range (12 km) have very small elephants (S_i

315   ≤ 0.20). There is no trend (p=0.08) for increased dwarfism on islands further away

316   than 48 km (the maximum reported distance covered by swimming for Asian

317   elephants in Johnson [1980]).

318   Log surface and log surface alternative are very strongly correlated with each

319   other (Pearson R=0.96, p<0.01) and with S_i (Pearson R=0.48, p<0.05 and 0.53,

320   p<0.05, respectively). Based on this result, we proceeded with the first only, because

321   this is considered the most reliably estimated value for any given island. The

322   correlation between island area and body size index is positive but weak, with area

323   explaining only 23% of the total variance (r^2=0.23, p=0.02). The residuals show no

324   correlation with latitude (r^2=0.02, p=0.52). The residuals for *Stegodon* only, however,

325   show a single outlier: *S. aurorae* from Japan. The difference from the predicted value

326   is -0.26 compared to -0.17–0.09 for the other species. *Stegodon aurorae* occurred at a

327   much higher latitude as compared to all other *Stegodon* species. Considering the three

328   genera separately, the correlation is stronger and more significant for *Stegodon*

329   (r^2=0.83, p<0.01; with the tentative exclusion of the Japanese stegodont based on

330   latitude) than for all taxa taken together.

331   The effect of competition (Table 2) on body size variation of proboscideans is

332   limited (on average, S_i=0.41 with competitors against S_i=0.17 without competitors)

333   but significant (p<0.01). Within the group lacking competitors, there is one less size-

334   reduced species (*S. florensis florensis*, S_i =0.51). This species is a 700 kyr older

335   chronosubspecies of the much smaller form (*S. florensis insularis*, S_i=0.17).

336   The effect of predation remains unclear. Given the lack of large terrestrial

337   predators on the focal islands (except for three or five islands, depending on whether

338   hominins can be considered as effective predators; Table 2), we were unable to assess

339   the potential effect of predation on body size variation of these very large mammals.

340   However, between species that occur on the same island but during a different time

341   period, the species with predators show a smaller size reduction than the species

342   without predators. This is shown by *P. mnaidriensis* versus *P. falconeri* and perhaps

343   by *S. florensis* versus *S. sondaari*. Admittedly, a different geological period likely

344   implies different vegetation, area, isolation etc. as well, so the interpretation of this

345   observation is tentative.

346

347 **DISCUSSION**

348 **Temporal variation in body size of proboscideans**

349 Fossil proboscideans exhibit much more extreme cases of dwarfism than living

350 species (less than 5% the body mass of their ancestors; Fig. 1). One plausible

351 explanation is that these differences in degrees of body size evolution between extant

352 mammals and those studied here is simply a function of the much more extended

353 geological period over which the evolutionary change could be analysed in the fossil

354 record, rather than the comparatively short time span of ~ 15 kyr since the last sea-

355 level rise during which size reduction occurred in most extant mammals occurring on

356 continental islands, as was also suggested by Lomolino *et al.* (2013).

357

358 **Factors associated with body size variation in proboscideans**

359 Body size reduction in proboscideans appears to be most pronounced for the species

360 occurring on the most isolated palaeo-island: *P. falconeri* of south-eastern Sicily,

361 whether its isolation is 100 km or 200 km. Yet, when considering all species together,

362 no significant correlation was found between isolation and the degree of body size

363 reduction. A possible explanation for the lack of a correlation may be that isolation

364 per se is not a good estimator for accessibility. For example, despite the great

365 distance, Sulawesi appears to have been comparatively "easy" to colonize, if we take

366 into account the comparatively large number of terrestrial immigrants that were able

367 to cross Makassar Strait: apart from murine rodents, also squirrels, bovids, suids,

368 macaques, and hominins reached Sulawesi at some stage prior to the late Pleistocene

369 (de Bruyn *et al.*, 2014; G.D. van den Bergh *et al.*, in press). These are all clades that

370 are not typical island taxa. It is likely that prevailing oceanic currents are a major

371 factor in determining island accessibility (Ali & Huber, 2010), but these are difficult

372 to incorporate into a generalized isolation index. Similarly, despite the relatively small

373 distance between Flores and the mainland (one or two crossings with visibility of the

374 target island) the strong Indonesian through-flow currents (Sprintall *et al.*, 2014) that

375 pass through these gaps may have significantly undermined overseas dispersal to

376 Flores.

377 Body size appears positively but weakly correlated with island area for

378 proboscideans as a whole. The relation is much more robust for *Stegodon*, if we

379 exclude the most northern species (*S. aurorae*), which appears much smaller than

380 would be predicted, and the earlier chronosubspecies of Flores (*S. florensis florensis*).

381 Our results provide only limited support for a direct influence of predation on

382 body size of insular proboscideans (but see Meiri's *et al.*'s [2008b] account of

383 dwarfism in extant, large mammals, which may have been associated with reduced

384 predator pressures of Borneo). This may stem at least in part from the limited

385 variability in predator assemblages on the islands we studied. Nevertheless, temporal

386 variation in ecological assemblages on Flores reveals the lack of a significant effect of

387 predators on body size evolution of native stegodonts in the long run. Here, a

388 geologically older pygmy stegodont (*Stegodon sondaari*) was replaced by a larger

389 stegodont (*S. florensis*), coinciding with the arrival of a hominin. The latter apparently

390 had access to carcasses as attested by cut marks on stegodont bones in the site Liang

391 Bua (van den Bergh *et al.*, 2009). Yet, even with this putative predator around, the

392 larger *Stegodon* decreased in size between the middle Pleistocene (Soa Basin;

393 subspecies *florensis*) and the latest Pleistocene (Liang Bua; subspecies *insularis*) (van

394 den Bergh *et al.*, 2008), and eventually its degree of dwarfism practically rivalled that

395 of *S. sondaari* (S_i=0.17 and 0.15 respectively). It seems, thus, that the effect of

396 predation on proboscideans was either modest or, perhaps more likely, a function of

397   the diversity and intensity of predators. After all, a single, hominin predator is likely

398   not as significant as an assemblage of large felids and other mega-carnivores as

399   present in mainland settings. In addition, *Stegodon* predation by hominins on Flores

400   may have been a relatively late development, since there are no indications for active

401   hunting or butchering of stegodont remains in the various middle Pleistocene

402   assemblages from the So'a Basin (van den Bergh *et al.*, 2014).

403   The presence of other large herbivores on the other hand has a significant

404   influence on the degree of dwarfism of insular elephants. Species with other

405   proboscideans as a competitor all show a less dramatic size reduction than species

406   with other competitors or no competitors at all. The strong influence of competition

407   on body size evolution is in line with the model of Lomolino *et al*. (2012), and was

408   also noticed for Mediterranean elephants by Palombo (2009).

409

410   **CONCLUSIONS**

411   This study provides further support for the applicability of the island rule to the

412   largest terrestrial mammalian herbivorous taxa (see Benton *et al.* [2010] and Stein *et*

413   *al*. [2010] for intriguing indications that very large herbivorous dinosaurs such as

414   titanosaurian sauropods may have also followed the predicted pattern).

415   The patterns discussed here for body size variation of proboscideans over

416   space and time do not support a significant relation between isolation and body size

417   decrease for proboscideans. Islands relatively close to the mainland may harbour

418   extremely size-reduced proboscideans as well as normal-sized species. Islands further

419   away than 48 km (the maximum reported distance an Asian elephant can swim) do

420   not harbour the smallest species.

421   The correlation between area and body size is positive but weak with much

422   scatter around the trend for all proboscideans but more robust for *Stegodon* from low

423   latitude islands. Our observations support an ecological hypothesis of body size

424   evolution, inferred from the significant influence of competition on body size

425   evolution (see also Palombo, 2009). On the mainland and on relatively balanced and

426   ecologically rich palaeo-islands such as Sulawesi, interaction with ecologically

427   relevant species resulted in a (relatively) large body size. On islands with more

428   depauperate assemblages, however, release from these ecological interactions appears

429   to have resulted in a smaller body size. In the absence of competitors, body size tends

430   to trend towards a size positively correlated with island area, provided that deep

431   geological time was available to allow the dwarfing process to proceed beyond the

432   initial phases.

433

434   **ACKNOWLEDGMENTS**

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652

653   **SUPPORTING INFORMATION**

654   Additional Supporting Information may be found in the online version of this article:

655   **Appendix S1** Body mass estimations of palaeo-species, palaeo-island characteristics

656   and statistical analyses.

657   **BIOSKETCH**

658   **Alexandra A.E. van der Geer** is a palaeontologist and first author of *Evolution of*

659   *island mammals: adaptation and extinction of placental mammals on islands*. Her

660   current research focuses on evolutionary processes on islands, including body size

661   evolution and morphological changes in the skeleton. Author contributions: A.V.G.,

662   G.A.L., G.v.d.B conceived the ideas, planned the analysis and analysed the data;

663   G.A.L., G.v.d..B., U.W., R.D.A., E.S. collected the data; G.A.L. prepared the figures;

664   and A.V.G. led the writing assisted by G.A.L., G.v.d..B., U.W., R.D.A., E.S. and H.D.

665

666   Editor: Robert Whittaker

667

TABLES AND FIGURE CAPTIONS

Table 1 Variation in body mass indices (**S**$_i$ as a proportion of ancestral body size) of insular proboscideans in alphabetical order of species name. Body mass estimations were based on postcranial elements (humerus, femur, tibia) using the equations of Christiansen (2004) for *Mammuthus, Palaeoloxodon* and for *Stegodon* species for which these elements were available. For *Stegodon* species of which only (fragments of) adult mandibles were available, body mass estimates were based on a regression between log-transformed postcranial-based average body mass estimates and average mandibular width measurements of adult specimens (M18 of van den Bergh, 1999; only mandibles were used in which the last molar was in function), with body mass as the 'dependent' variable. This method was developed based on *Stegodon* species for which both variables were available based on averages of more than 1 specimen (Appendix S1). Indices based on the lower third molar (M$_3$) are calculated as the ratio of the cubed linear dimensions, following Lomolino (2005). Although this method likely overestimates body size of large-sized insular forms, it appears reliable in small-sized phylogenetic dwarfs (see for a discussion on teeth and body size reduction of phylogenetic dwarfs in Lister, 1996 and Appendix S1). The species indicated with an asterisk is an older chronospecies preceding the smaller form. Sources for *S*$_i$: 1=van den Bergh, 1999; 2= Lomolino *et al.*, 2013; 3= this study, based on M=mandible, P=postcranial, or T=third molar (see Appendix S1 for specimens, method and details); 4 = van der Geer *et al.*, 2014. The "large-sized *Elephas*" from Sulawesi (Tanrung Formation) might be *P. namadicus*. No complete long bones or third molars were found, but according to van den Bergh (1999) the

691 size of a molar fragment falls within the size range of *P. namadicus*, hence its body

692 size index is tentatively taken here to be 1.0. This may be an over-estimation in case

693 size decrease had just begun. For calculation of area and isolation at sea level 60 m

694 below present, see Appendix S1. Geological age: EP=early Pleistocene, MP=middle

695 Pleistocene, LP=late Pleistocene, H=Holocene.

Palaeo-island	Species	Mainland ancestor	S_i	Source	Area (km2) / isolation (km)	Geological age
Crete	*Mammuthus creticus*	*M. meridionalis*	0.04	2	(4175 or 8350) / 90	EP
Santa Rosae	*Mammuthus exilis*	*M. columbi*	0.17	2	2200 / 10	LP
Sardinia	*Mammuthus lamarmorai*	*M. meridionalis*	0.08	2	26343 / 50	LP
Wrangel	*Mammuthus primigenius*	*M. primigenius*	0.47	2	7600 / 140	H
Sicily	*Palaeoloxodon 'mnaidriensis'*	*P. antiquus*	0.17	2	23000 / (1 or 4)	late MP-early LP
Crete	*Palaeoloxodon creutzburgi*	*P. antiquus*	0.38	2	9460 / 90	LP
Kassos	*Palaeoloxodon 'creutzburgi'*	*P. antiquus*	0.30	3 (T)	600 / 50	LP
Cyprus	*Palaeoloxodon cypriotes*	*P. antiquus*	0.02	4	9234 / 69	LP
Sicily	*Palaeoloxodon falconeri*	*P. antiquus*	0.02	2	(2200 / 200) or (11600 / 100)	early MP
Naxos	*Palaeoloxodon lomolinoi*	*P. antiquus*	0.08	4	1226 / 30	LP
Rhodos	*Palaeoloxodon* sp.	*P. antiquus*	0.19	4	1660 / 15	LP?
Sulawesi	*Palaeoloxodon* sp. ("large-sized *Elephas*")	*P. namadicus*	~1.00	1	174600 / 50	MP
Tilos	*Palaeoloxodon tiliensis*	*P. antiquus*	0.09	2	116 / 15	LP
Japan	*Stegodon aurorae*	*S. zdanskyi*	0.25	3 (P)	263237 / 20	EP
Flores	*Stegodon florensis florensis**	*S. ganesa*	0.51	3 (P)	21910 / (45 or 225)	MP
Flores (Liang Bua)	*Stegodon florensis insularis*	*S. ganesa*	0.17	3 (P)	21910 / (45 or 225)	LP
Luzon	*Stegodon luzonensis*	*S. ganesa*	0.39	3 (T)	(157000 or 59250) / (45 or 65)	LP
Sulawesi	*Stegodon sompoensis*	*S. ganesa*	0.32	3 (M)	(174600 or 24020) / 50	EP

Flores (So'a Basin)	*Stegodon sondaari*	*S. elephantoides*	0.15	3 (P)	21910 / (45 or 225)	EP
Sulawesi	*Stegodon* sp. B	*S. ganesa*	0.57	3 (T)	174600 / 50	MP
Sumba	*Stegodon sumbaensis*	*S. ganesa*	0.08	3 (M)	3250 / 119	MP–LP
Timor	*Stegodon timorensis*	*S. ganesa*	0.23	3 (M)	10560 / 78	MP
Java (Trinil H.K.)	*Stegodon trigonocephalus*	*S. ganesa*	0.65	3 (P)	138794 / (1 or 4)	late EP

696

697 **Table 2** Presence of ecologically relevant competitors and predators for the insular

698 species mentioned in Table 1. Predators less than c. 15 kg (e.g. otters, foxes) are not

699 considered potentially relevant for proboscideans and omitted here. EP = early

700 Pleistocene, MP = middle Pleistocene, LP = late Pleistocene, P = Pleistocene (no

701 further stratigraphical evidence), H = Holocene.

Species	Palaeo-island	Geological time	Competitors	Predators
E. sp.	Sulawesi	MP	Elephant (*Stegodon* sp. B), bovid? (*Bubalus depressicornis*), suid? (*Celebochoerus* sp.)	-
M. creticus	Crete	EP	-	-
M. exilis	Santa Rosae	LP	-	-
M. lamarmorai	Sardinia	LP	Deer (*Praemegaceros cazioti*)	-
P. creutzburgi	Crete	LP	Deer (*Candiacervus* spp.)	-
P. aff. *creutzburgi*	Kassos	LP	Deer ("*Candiacervus*" sp.)	-
Palaeoloxodon cypriotes	Cyprus	LP	-	-
P. falconeri	Sicily	early MP	-	-
P. 'mnaidriensis'	Sicily	late MP–LP	Deer (*Cervus elaphus, Dama carburangelensis?*), bovids (*Bos primigenius, Bison priscus*)	Hyena (*Crocuta crocuta*), wolf (*Canis lupus*)?
P. sp.	Rhodos	LP?	-	-
P. lomolinoi	Naxos	LP	-	-
P. tiliensis	Tilos	LP–H	-	-
S. aurorae	Japan	EP	Deer (*Elaphurus* spp., *Cervus* sp.), rhino (*Rhinoceros* sp.)	wolf (*Xenocyon falconeri*)
S. florensis florensis	Flores	MP	-	hominin (*Homo floresiensis*)?
S. florensis insularis	Flores	LP	-	hominin (*Homo floresiensis*)?

| *S. luzonensis*	Luzon	P	Elephants (Proboscidea indet., *Elephas beyeri*), deer (*Cervus* sp.), rhino (*Rhinoceros luzonensis*)	-
S. sompoensis	Sulawesi	EP	Elephant (*Stegoloxodon celebensis*), suid (*Celebochoerus heekereni*)	-
S. sondaari	Flores	EP	-	-
S. timorensis	Timor	MP	-	-
S. sp. B	Sulawesi	MP	Elephant (*Elephas* sp.), bovid? (*Bubalus depressicornis*), suid? (*Celebochoerus* sp.)	-
S. trigonocephalus	Trinil (Java)	late EP	Deer (*Axis lydekkeri, Rusa timorensis*), large bovids (*Bubalus palaeokerabau, Epileptobos groeneveldti, Bibos palaesondaicus*), elephant (*E. hysudricus*), rhino (*Rhinoceros sondaicus*)	Tiger (*Panthera tigris*), hyena (*Pachycrocuta brevirostris*), hominin (*Homo erectus*)?
S. sumbaensis	Sumba	MP–LP	-	-

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705 **Figure 1** Reconstruction of four insular dwarf proboscideans with their respective

706 mainland ancestors . Mainland proboscideans: 1, *Palaeoloxodon antiquus*; 2,

707 *Mammuthus columbi*; 3, *Stegodon zdanskyi*. Insular proboscideans: 4, *Palaeoloxodon*

708 '*mnaidriensis*'; 5, *Palaeoloxodon falconeri*; 6, *Mammuthus exilis*; 7, *Stegodon*

709 *aurorae*. Based on skeletons at Museo di Paleontología, University of Rome, Italy (1),

710 American Museum of Natural History, New York (2), Taylor Made Fossils, U.S. (3),

711 Museo di Paleontología e Geología G.G. Gemmellaro, Palermo, Italy (4),

712 Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (5), Santa

713 Barbara Museum of Natural History, Santa Barbara, U.S. (6), Taga Town Museum,

714 Honshu, Japan (7). Photos 1–2, 4–7 George Lyras, photo 3 courtesy of

715 TaylorMadeFossils.com, reproduced here with permission.

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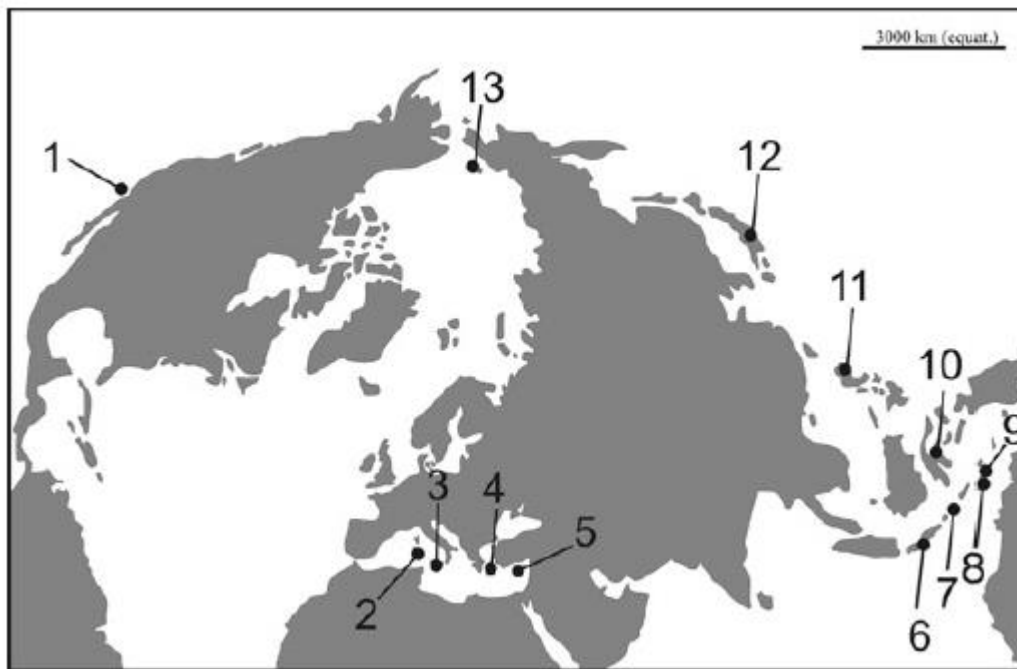
717

718 **Figure 2** Simplified map showing the geographical position of the islands with insular

719 Proboscidea used in this study. 1, California Channel Islands; 2, Sardinia; 3, Sicily; 4,

720 Islands of the Aegean (Crete, Karpathos, Palaeo-Cyclades, Rhodos); 5, Cyprus; 6,

721 Java; 7, Flores; 8, Sumba; 9, Timor; 10, Sulawesi; 11, Philippines; 12, mainland Japan

722 and the Ryukyu Islands; 13, Wrangel. The coastline is based on a map from d-

723 maps.com.